THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

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(*Continued from p. 186.*)

Soil.—Of great importance as an ecological factor is the composition of the soil, physical and chemical. Contrary to the popular belief, the former is at least as important as the latter.

In its physical composition the marsh soil is remarkably homogeneous. Samples taken from the most diverse situations, from the newest layers brought in by the tides, from old long-cropped marsh, from dredgings deep beneath the bogs, are all so alike as to be indistinguishable except for a variation from red to blue in color, and, probably, a somewhat coarser texture of the soil along the banks of the rivers. It is very important to remember, also, that the soil is very deep, even to eighty feet, though usually much less than this. A combination of so homogeneous with so deep a soil must be rare.

In its general characters the dry marsh soil is light brownish red in color, and extremely fine grained in texture. So fine grained is it that only rarely are the individual grains visible to the naked eye. It has no appearance of humus but rather somewhat suggests clay. When the newly deposited layers are exposed to the sun, they harden enough to require a sharp blow to break them, and crack into polygonal areas, concave upward, from a few inches up to two or three feet in diameter, the cracks often being several inches deep and an inch across. When protected from the direct sun, as on the reclaimed marsh, the caking and cracking is much less marked. When again wetted, however, the hard layers melt away into their former state. It sometimes happens on newly plowed ground that a heavy rain

followed by bright sunshine will cause the surface to cake so hard that germinating seeds cannot break through, and much loss is thus caused to crops.

The mechanical nature of the soil will be much more evident from the following mechanical analysis of five selected samples from typical localities, which has been made for me through the kindness of Professor G. E. Stone, of the Massachusetts Agricultural College.

Samples	Water	Organic Matter	Gravel, 2–1 mm Diam.	Coarse Sand, 1–0.5 mm	Medium Sand, 0.5–0.25 mm	Fine Sand, 0.25–0.1 mm	Very Fine Sand, 0.1–0.05 mm	Silt, 0.05–0.01 mm	Fine Silt, 0.01–0.005 mm	Clay, 0.005–0.001 mm	Total
I. Timothy marsh, unplowed for 40 years....	2.200	6.505	.025	.275	4.125	9.360	22.185	36.165	10.390	8.585	99.815
II. Low marsh, with poor vegetation............	2.600	10.920	.000	.400	.285	1.900	1.300	50.110	17.735	10.530	[24] 95.780
III. Brought in freshly by tide...............	1.800	6.200	1.125	3.100	2.025	4.225	45.275	14.125	12.400	9.660	99.935
IV. Blue mud from 18 inches under surface...	3.160	7.360	.125	.325	2.400	6.210	33.885	20.375	10.865	15.200	99.905
V. From River Habitant, N.S.[23]...............	3.400	3.200	.125	.260	1.485	4.060	46.010	26.800	8.710	5.825	99.875

These figures confirm the impression made by the appearance of the marsh soils, that they are, as a whole, of unusually fine texture. This becomes yet more evident when they are compared with the results of similar analyses made of various soils elsewhere (as for example the many published in the *Bulletins* of the Division of Soils of the United States Department of Agriculture).[25] Soils of this degree of fineness are far from those adapted to truck and root crops, and are close to those best adapted for grass and grain crops. The fineness of the soil, with its consequent increase of surface for chemical solution, has an important influence upon its fertility, in rendering more easily available such valuable minerals as it possesses. The marsh soils differ, however, from most other fine soils in the smallness of the proportion of clay in comparison with the silt and fine silt. A

[23] A specimen sent me by Professor Shutt.

[24] Obviously a considerable error here; cause unknown. Probably the entire analysis of this sample is untrustworthy.

[25] Or the synoptical article, "Soils in their relation to crop production," by Milton Whitney, in the Year Book of the U. S. Department of Agriculture for 1894.

microscopical examination of the soil shows that it consists of irregular, very angular grains of many different colors and sizes. Very marked and characteristic, in every one of the very many samples of the soil examined, is the occurrence of fragments of sponge spicules, some of the more marked forms of which are shown in *fig. 6.* While these spicules do not form any considerable part of any particular sample, certainly not 1 per cent., nevertheless their aggregate quantity in the enormous deposit of marsh mud is very great, supposing, as the samples indicate, they are distributed everywhere through it. I do not imagine, however, that their presence has any significance whatever in the ecology of the vegetation.[26] Numerous diatoms of several forms are also present in the mud.

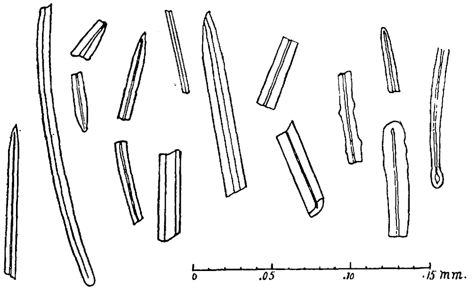

FIG. 6.—Typical forms of sponge spicules from the marsh mud.

The mechanical composition of a soil is important chiefly because of its relation to the supply and circulation of air and water through it. The finer a soil is, other things being equal, the better will it hold water in the hygroscopic state, and hence the better it is for the constancy of water supply to the vegetation. But on the other hand the finer it is the less air will it hold and allow to circulate, and air (*i. e.*, the oxygen) necessary for the respiration of roots is well-nigh as essential a constituent of the soil as water. The soil of the marshes, being much finer than the average, is better than the average for holding and delivering

[26] I think they are without doubt spicules, though they are very fragmentary. They are insoluble in the ordinary acids, and hence are probably siliceous. Very similar forms are figured in the Challenger Report II: *pl. 3, fig. 6*, though I have not seen any branched forms. Two sources of supply are imaginable; living sponges in the Bay and the fossils in the Permo-Carboniferous rocks. But the water must be too muddy for living sponges to flourish, and, moreover, the spicules are very fragmentary, as would be expected if they are ground forcibly out of the rocks, but not if they are floated up from the decay of sponge bodies. Dr. G. F. Matthew tells me fossil sponges are not known from the Permo-Carboniferous rocks.

water, but is worse than the average for aeration. For the latter reason it is adapted only for vegetation with superficial or extremely slender roots, and such the grasses are, while thick-rooted forms, like trees or root crops, needing better aeration, cannot grow, or at least cannot thrive, there.

An extremely important property of soils is their power of circulating water and mineral matters. Every particle of moist soil is surrounded by its film of hygroscopic (and capillary) water holding mineral matters in solution, and these films are in continuity. But the relations of these films to the soil particles and to one another are such that they are, as it were, in a state of unstable equilibrium, so that when water is removed (if not too rapidly) from them at any place, it is restored from neighboring particles, which draw upon others yet more remote, and so on until the equilibrium is restored. And this adjustment is the more perfect the finer the soil. When thus traveling the water carries its dissolved minerals with it. Moreover, owing to the operation of the process of diffusion, the minerals are tending to distribute themselves through the films of water even when these are at rest, from the places where the minerals are more abundant to the places where they are less so. The law of water and mineral movement in soils may be thus expressed: *In a homogeneous soil the water tends to distribute itself evenly throughout the mass, and the soluble minerals tend to distribute themselves evenly throughout the water; a draft at one place upon water and minerals therefore is a draft upon the entire mass if the rate of removal be not more rapid than the equilibrium-restoring power of the soil, which is the higher the finer the soil.* It hence follows that in a homogeneous or nearly homogeneous soil, the plants, if their demands be not greater than the power of the soil to distribute the water, are not dependent for water and minerals simply upon such parts of the soil as can be reached by their roots, but can draw upon the entire mass, the more readily the finer the soil is. Here, I believe, we find the explanation of the lasting quality of the fertility of these marshes when reclaimed; it is due to their depth in combination with their homogeneity, aided by the great water-holding and transferring power given by their fineness of soil. The abundant water

falling upon them as rain, or derived from the melting snows in spring, must saturate the soil to considerable depths, if not to the bottom, thus bringing the water and minerals of upper and lower levels into continuity. Now there is no circulating ground water in the marshes, as the invariable failure of wells dug upon the marshes shows; furthermore they lie below the level of the fresh water of the bogs and mostly below the high-tide level of the sea, and hence there can be no under-marsh drainage, no more indeed than the surface drainage allowed by the shallow ditches or natural runways. This lack of deep drainage has two important consequences; first, there is little or none of that loss of the valuable soluble mineral matters such as is constantly occurring on well-drained upland soils (a fact which alone goes far to explain the lasting fertility), and second, practically the only outlet for the water of the soil is by evaporation from the surface or transpiration through the plants, both of them necessitating an upward movement which tends to bring up the minerals from below. That this effect is actually produced by evaporation is shown by the fact that bald spots even on long-reclaimed, and hence long-drained, marsh always show an efflorescence of salt, and the same is true upon all freshly-exposed surfaces of marsh mud, no matter how long this may have been shut off from the sea. These facts can only be explained by supposing that the salt is brought up constantly from the greater depths. Further, practically the entire vegetation of the marshes consists of the grasses, which both have a comparatively low rate of transpiration themselves, and also protect the ground in an unusual degree from direct evaporation. Hence the upward movement is but slow, and when the warm summer sun promotes transpiration from the plants, the draft made upon the water of the upper soil is not too rapid to allow the latter to recoup itself from the lower layers, and that from a still lower, and so on, to a considerable or even great depth. This upward movement brings with it the minerals, which are not only thus being lifted towards the surface by the ascending water streams, but are constantly diffusing from the lower richer to the upper poorer layers. It can thus come about that the entire depth of the marsh soil is available to the vegeta-

tion above, and it would be only when the minerals from the entire depth are exhausted that the fertility would begin to fail. A corollary of this would be that those marshes whose fertility is most lasting are the deepest, and those soonest exhausted are the shallowest, which certainly agrees in general with the actual facts, as observed and related by those familiar with the marshes.

It is possible that the bogs, which in places underlie the marshes, play some part in this question of water conditions, but we have no facts bearing on this question. As already mentioned, the borings made in the Aulac marsh showed twenty feet of bog lying beneath the eighty feet of marsh mud. Mr. Chalmers is of the opinion that bogs extend practically everywhere beneath the marsh, but I do not think this is probable. If the mode of formation of the marshes in the earlier stages, given earlier in this paper, is correct, it is plain that the marsh could have formed without covering any bog except that which may have existed in the fresh-water lake in this basin before marsh-formation began. Bogs, however, could be buried under mud through natural changes in the courses of the rivers, and they are now often buried in the operations of bog-reclamation. Such places are said to be better drained and to bear larger crops than similar marsh not underlaid by bog.

There are other physical properties of soil of much importance to the vegetation occupying it, such as its permeability to air, its power of absorbing and retaining heat, etc., but for the marsh mud no data at all are available upon these properties.

We pass next to consider the chemical composition of the marsh soil, upon which some satisfactory data are available. Five samples carefully collected by myself in 1898 from different typical situations on the marshes, and of four of which the mechanical analyses have been given on an earlier page (281), have been carefully analyzed for me by the courtesy of Professor Frank T. Shutt, chief chemist at the Chemical Laboratory of the Dominion Experimental Farm at Ottawa, with the following results.[27] To these are added an analysis made at the same lab-

[27] A full discussion of these analyses by Professor Shutt may be found in the Report for 1901, cited in the Bibliography.

oratory, of a similar marsh soil from Cornwallis Valley, Nova Scotia:

SAMPLES	Organic and Volatile Matter	Clay and Sand	Oxid of Iron and Alumina	Lime	Magnesia	Potash	Phosphoric Acid	Soluble Silica
I. Timothy marsh, unplowed for 40 years....	6.54	75.29	14.72	.239	.513	.817	.136	.091
II. Low marsh, with poor vegetation............	10.60	73.18	12.64	.234	.397	.852	.124	.059
III. Brought in fresh by the tide	6.02	75.83	13.79	.652	..283	.902	.146	.063
IV. Blue mud from 18^{in} under surface.........	6.77	76.01	14.01	.409	.183	.996	.094	.056
V. From 30^{in} below surface under canal above Point de Bute	3.10	84.48	9.87	.288	.154	.646	.110	0.63
VI. From River Habitant, N. S.................	4.14	75.59	11.71	1.40	.48	.25	.15	......

SAMPLES	Carbonic Acid, &c., Undetermined	Total	Nitrogen	AVAILABLE.[28] Potash	AVAILABLE.[28] Phosphoric Acid	AVAILABLE.[28] Lime	Reaction	Common Salt
I. Timothy marsh, unplowed for 40 years....	1.654	100.0	.182	.0088	.026	.0626	Acid.	.037
II. Low marsh, with poor vegetation............	1.914	100.0	.338	.034	.016	.0449	Acid.	1.048
III. Brought in fresh by the tide	2.314	100.0	.122	.0748	.0466	.397	(*)	4.16
IV. Blue mud from 18^{in} under surface.........	1.472	100.0	.106	.0073	.0436	.0792	Acid.	.939
V. From 30^{in} below surface under canal above Point de Bute	1.289	100.0	.062	.030	.0354	.108	Acid.	.217
VI. From River Habitant, N. S.................	......	......	.128	.06	.05	......	......	.86

An abstract of the remarks made upon the samples by the analyst is as follows:

No. I. As to humus (organic matter) nitrogen and lime, about as in soils of average fertility; potash in this as well as the others, much higher than in

[28] The "available" quantities are attained by the Dyer citric acid method. Compare the report by Shutt, just mentioned.

* Neutral or slightly alkaline.

most virgin soils, existing probably as double silicates likely to be gradually liberated in available form by good culture and favorable climatic conditions; phosphoric acid somewhat lower than in virgin soils of average fertility, but a large amount of it is in available form; oxide of iron large in amount, a favorable feature for fertility under proper cultivation; immediately available potash not abundant in this sample, probably because removed for so many years by the hay crop, but available phosphoric acid fairly abundant.

No. II. Shows nearly double the organic matter and nitrogen of no. I; also much richer in potash, total and available, but has less phosphoric acid. If properly drained should give results as good as no. I.

No. III. Of special interest as showing the composition of the original soil as brought in by the tide. Shows nearly three times the lime of nos. I and II, no doubt because so much lime has been removed from the former with the crops.

No. IV. Not positively deficient in substances needful for fertility but mechanically unfavorable. (Compare remarks on these blue soils on the next page.)

No. V. Not appreciably different from the others except in its smaller proportion of nitrogen and humus, which is explained by its deeper position.

No. VI. Not richer in mineral matters than many soils of average productiveness. But a discrimination between the total amounts of the important substances, and the amounts immediately available, shows a remarkably large proportion of the latter, as compared with other fertile soils, and probably in this feature consists a large part of its richness.

With these it is of interest to compare an earlier, and apparently careful, analysis given by Dawson, in his *Acadian Geology* (third edition p. 23) of a "Red soil from Truro, recently deposited":

Moisture	.5		Organic matter	1.5
Soluble in water			Carbonate of lime	3.60
Chlorine	.095	as common salt	Oxide of iron	2.74
Soda	.115	as common salt	Alumina	1.20
Potash	.013		Magnesia	.11
Sulphuric acid	.073	as gypsum	Soda and potash	.8
Lime	.061	as gypsum	Phosphoric acid	.09
Alumina	.005		Siliceous sand (very fine)	88.00
Magnesia	.004			

Trueman gives some analyses, very imperfect, however, of these soils in his paper (page 104),[29] and some others are found

[29] Eaton, in his most excellent account of the marshes, points out what he thinks a chemical difference between the marshes of Minas Basin and those of Chignecto Bay in that the former contain larger quantities of salts of potash, lime and alumina.

in the various reports of the chemist of the Experimental Farm, cited in the Bibliography.

The marsh soil, however, is not always red and rich, but it is in places blue and barren. This blue soil occurs in low badly drained places, is but a few inches deep, and is underlaid by red soil, which occurs everywhere in a layer under the bogs. Bands of it appear occasionally on river banks in the rich well-drained marsh; but, as already pointed out, this is without doubt due to the wandering of the rivers, which, in changing their courses, cut into spots previously back from their courses and badly drained. The blue soil seems, however, at times to underlie the "sedge-bogs" along the rivers. A full account of the formation of this blue soil is given by Dawson in his *Acadian Geology* (p. 24 of the third edition) as follows:

The chemical composition of this singular soil, so unlike the red mud from which it is produced, involves some changes which are of interest both in agriculture and geology. The red marsh derives its color from the peroxide of iron. In the gray or blue marsh the iron exists in the form of a sulphuret, as may easily be proved by exposing a piece of it to a red heat, when a strong sulphurous odor is exhaled, and the red color is restored. The change is produced by the action of the animal and vegetable matters present in the mud. These in their decay have a strong affinity for oxygen, by virtue of which they decompose the sulphuric acid present in the sea-water in the forms of sulphate of magnesia and sulphate of lime. The sulphur thus liberated enters into combination with hydrogen obtained from the organic matter or from water, and the product is sulphuretted hydrogen, the gas which gives to the mud its unpleasant smell. This gas dissolved in the water which permeates the mud, enters into combination with the oxide of iron, producing a sulphuret of iron, which with the remains of the organic matter, serves to color the marsh blue or gray. The sulphuret of iron remains unchanged while submerged or water soaked, but when exposed to the atmosphere, the oxygen of the air acts upon it, and it passes into sulphate of iron or green vitriol—a substance poisonous to most cultivated crops, and which when dried or exposed to the action of alkaline substances deposits the hydrated brown oxide of iron. Hence the bad effects of disturbing blue

These substances he supposes to be derived from the trap rocks at the entrance to Minas Basin, which rocks are absent on the Chignecto Branch. Hence he says, the Minas marshes have shown no signs of exhaustion, while the Chignecto marshes have. Comparative analyses of samples from both sets of marshes as far as available do not sustain this contention, nor, indeed, as far as I can learn, is he correct in his estimate of the relative lastingness of the fertility of the two sets of marshes.

marsh, and hence also the rusty color of the water flowing from it. The remedies for this condition of the soil are draining and liming. Draining admits air and removes the saline water; lime decomposes the sulphate of iron and produces sulphate of lime and oxide of iron, both of which are useful substances to the farmer.* [*Since the publication of the first edition of this work, the blue marsh of Nova Scotia has been extensively improved by this process.]

Grouping together the facts as to chemical composition, it is plain that the marsh soil as a whole is rather uniform in composition; that it is chiefly composed of fine siliceous sand with an average of about 10 per cent. of clay; that it naturally contains but little organic matter, which only develops sparingly with the denser vegetation of the reclaimed marsh; that it contains percentages of potash, lime, phosphoric acid, and nitrogen, approximating those of good virgin soils elsewhere, but with an unusually large amount of those substances in an immediately available form; and that the amount of common salt varies with the degree of reclamation. The above facts amply explain the fertility of the marshes, more especially when it is remembered that the chief, almost the sole, crops are grasses, which are not very trying to the soil, and to which the above combination of substances and conditions is particularly favorable. The lasting quality of the marshes is not thus explained, but that, as I have earlier shown, is without much doubt due to their depth and homogeneity, whereby the entire mass to the bottom is made available to the vegetation. These two sets of factors together, I believe, amply explain the agricultural value of the marshes.[30] The composition of the marsh soil as a whole is doubtless very similar to that of the red sandstones of this region (with, perhaps, some salt added from sea-water), which constitute some of the richest upland soils in the provinces. The resemblance is

[30] There is in the marsh country a popular misunderstanding of this subject. It is customary for the residents to say that the analyses of the soil which have been made reveal only clay and sand, with nothing to explain its fertility, which they think must therefore be due to some cause still unknown. No doubt the smallness of the percentages of potash, lime, nitrogen, etc., mislead those unacquainted with the chemistry of soils. In fact the richest soils contain as a rule less than one per cent. of each of those important substances, and quantities much over one per cent., so far from making the soil richer, actually injure it, for the roots of plants are unable to absorb any but very weak solutions of mineral substances.

of course genetic, for the marshes are such soils pulverized and leveled by the sea.

The analyses show further the comparative poverty of the marsh soil in lime, certainly the greatest defect of the marshes, and this substance is the first which has to be added to degenerating marsh. This fact is of much importance ecologically, for to the absence of lime is due the possibility of the formation of sphagnum bogs so extensively developed with the marshes, the sphagnum not growing where lime occurs. The neighboring upland, composed of Carboniferous sandstones, also is free from lime.

The form of occurrence of nitrogen in a soil is very important to its fertility, and as to this the analyses give us no information. The amount of available nitrogen in a soil is closely correlated with the presence of bacteria, and here also, for the marsh soil, we have no data. The bacterial content is not likely to be large, however, since there is so little humus, on which they are dependent.

We must next consider a special phase of soil composition very important to our present subject, namely, the presence in it of common salt (sodium chlorid) derived from the sea water. In minute quantities (small fractions of 1 per cent.) salt in the soil, since it has no part in plant nutrition, does not appreciably affect vegetation as a whole, though it may influence individual forms; but when the percentage rises toward 1 per cent., its presence begins to be of consequence, while above 1 per cent. and upwards it produces profound effects upon the form and distribution of the vegetation. It acts both chemically and physically; chemically in that the plant cannot help absorbing it with the water and it affects injuriously some of the vital processes,[31] and physically because roots are unable to absorb water osmotically (their only method) where more than a very small amount of salt is present. With most roots water cannot be absorbed at all if it contain as much as 1 per cent. of salt and none can absorb it from a solution much, if any, stronger than 3 per cent. As to the amount of salt contained in the marsh soil,

[31] It can of course do this without acting positively as a poison; to what extent the salt is positively poisonous is still uncertain, though the studies of Loeb, True, and others seem to show that in some cases it is so.

that of course varies greatly, as the table on page 286 shows, with the degree of reclamation, etc., and it is this variation which is responsible for the profound differences in the vegetation of the different parts of the marshes. The water of the sea, which has everywhere laid down these marshes, and countless times has overflowed every part of them, must be very nearly the pure salt water of an open sea coast, that is, it must contain near 3 per cent. of salt. This is not only indicated by my tests (unhappily few and crude) of the density of selected samples (tested with an hydrometer), but also by the fact that the fresh-water streams of this region are comparatively insignificant in volume, and the swirling tides mix the fresh water thoroughly with the salt, preventing it from lying on the surface. Not only has every part of the marshes been as salt, or nearly, as the sea, but in places they are much salter, for, owing to the building up of the banks next the sea, there are many pools formed on the marshes into which the highest tides can run, but from which the water does not escape, remaining to evaporate and leave its salt. In many places on the unreclaimed marsh, especially between rivers, such pools exist, much too salt for any vegetation except a few simple algae; and it is quite probable that it is such former pools on the now reclaimed marsh which form the poor or bald places, later to be mentioned, so difficult fully to reclaim. On the other hand, although on the reclaimed marsh no new salt is being added, and the salt already there is being steadily removed by rains, by drainage, and with the crops, it appears never to be entirely removed, no doubt because it is constantly being renewed by diffusion, aided by evaporation, from greater depths. This is shown both by the analyses on page 287 where even the long reclaimed English hay marsh is shown to contain an appreciable amount, and other places a considerable amount, but also by the fact, well known in the marsh country, that an efflorescence of salt ("salt enough to taste," the residents say) is to be seen at times, after dry weather, on the surface of even the oldest reclaimed marsh. Further, the mud brought up from beneath the fresh-water bogs by the canal dredges, shows, as I have myself seen, a marked efflorescence of salt in drying. The

data as to the amount of salt in the reclaimed marsh are unfortunately scanty, but it seems safe to say that it must be on the best marsh much less than half of 1 per cent. and it grades from that upward in all degrees to the wild marsh, which may contain up to 4 per cent., or, in special places, considerably more. It is the presence of this salt even in the reclaimed marsh, which, more than any other cause, keeps the marshes treeless; the salt prevents that ready osmotic absorption essential to large vegetation.

The distribution of salt in the reclaimed marsh is not uniform, however, for places occur in which the vegetation exhibits markedly, or even extremely, a salt-marsh character. These places are of three sorts. First, there occur certain "bald spots," of no apparent determinants, on which only scanty salt-marsh plants grow, or, in certain cases, none at all. These may be remnants of ancient pools mentioned in the preceding paragraph. They can be rendered productive, however, which is effected by covering them with brush (branches of spruce, etc.), straw, loose boards, or other convenient material for two or three years, after which they bear the ordinary grasses of the surrounding marsh. Of course this comes about through the fact that the rain washes out the salt from this soil, and the ground being protected from evaporation, no new supply is brought to the surface by the rising water. Second, on marsh that is improperly drained, there are occasional low spots into which the rain settles from the neighboring higher parts, of course carrying with it some dissolved salt which is concentrated as the water evaporates, thus allowing only a salt vegetation. Third, the farm roads across the marshes, though little used, are always marked by lines of salt plants, often indeed in most striking contrast to the rich hay grasses on each side of them. The presence of the greater quantity of salt along the roads is due, I believe, to a cooperation of two causes; first, the travel over such roads tends to keep down the grasses and to leave the ground somewhat bare, so that evaporation from these places is much more rapid than from the neighboring densely grass-clad ground and the salt must therefore be drawn to the surface more abundantly

there than elsewhere; second, the travel tends somewhat to compact the soil on the roads, and evaporation is more rapid, other things being equal, from a compact than from a loose surface of a homogeneous soil, hence contributing to bring up the salt. In places, too, the roads are lower than the neighboring surface, so that water would tend to drain into them with its salt, which would be concentrated by evaporation; but this is not the main cause of the presence of the salt plants there, for they occur on high as well as low places. On the other hand, the places on the marshes which seem to become most free from salt are three. First, there are the dikes and the ridges thrown up in digging the ditches; the ditch-ridges in particular become so free of salt as to permit not only upland salt-shy weeds to grow but even the still more salt-shy bushes, such as alders, roses, etc. Their freshness is due, no doubt, in large part to the perfection of their drainage, but it is more the result, I believe, of the lack of homogeneous continuity between the somewhat loosely heaped ridge and the compact marsh soil, whereby the continuity of the hygroscopic soil water is interrupted and hence the upward movement by evaporation largely diminished. The comparative looseness and roughness of the ditch-ridges, also, like cultivation in a garden, lessens evaporation, which with the preceding factor permits the removal of salt here to be more rapid than its renewal. Second, there are the spots on good high marsh where hay-ricks have stood, on which a luxuriant weed-vegetation grows up. Plainly the causes are here as above indicated for the bald spots; the ricks preventing evaporation, there is no rise of salt to these places, but rather, by the movement of the water falling here as rain, a washing away of the salt to neighboring places. Much the same effect is produced by the shade of the barns. Third, there are occasional, though rare, spots on the high marsh, not in any way shielded from evaporation, on which weeds, and even small bushes, and in one case a small birch tree, stand. These places appear to me to be always on old and shallow marsh, and represent, I think, spots from which the salt has been in course of time largely removed by drainage and the crops.

Animals.—Animals through divers of their manifold activities may play a large part in phytoecology, but in the case of these marshes their influence appears with but one important exception to be insignificant. That exception is the animal commonly called man, who has developed the habit of providing himself with food by cultivation (in which respect he is by no means unique, but was long anticipated by the fungus-raising ants and others), and to this end has performed two operations of much importance in the ecology of the marshes: first, he has shut out the sea from great areas, thus allowing their conversion from a salt to a nearly saltless soil with the enormous change in their vegetation thus implied; and second, he has brought from other countries certain special kinds of plants which he has let run wild on these marshes. The latter point needs especial emphasis, since it is so liable to be misunderstood. A stranger, even a botanist, visiting for the first time the reclaimed marshes, and looking upon their extensive fields of rich grasses, is likely to think that they are kept in that condition only by careful sowing and frequent renewal, in the absence of which they would soon be replaced by other vegetation. This is what would soon happen on good upland hay fields, for instance, which soon revert to patches of wild weeds and later to forest. But such I believe would be not at all the fate of these marshes. It is of course true that if they were totally neglected by man, the drains would soon fill up, and the dikes would be broken down and washed away, after which the whole region would return to the condition of wild salt marsh. But if, in some way the dikes and drains could be made perpetual, I believe that the present English hay grasses could maintain themselves indefinitely, or at least as long as the fertility of the marshes lasts, without care from man, and they would not as a whole be replaced by any other vegetation. In other words, the English hay grasses brought in by man appear to be the very vegetation best adapted to the conditions prevailing on the reclaimed marsh, and no other, certainly no native plants, could drive them out. Many facts sustain this rather remarkable conclusion, of which the most important is this, universally stated

by those who work with the marshes, that when the marsh is diked and drained, a natural succession of plants follows the freshening of the marsh soil, ending with the English hay grasses, which come in of themselves without any artificial seeding or other aid whatever. They could not do this if there were other plants in the vicinity better adapted to the new conditions. Moreover, having once established themselves in this way, they maintain themselves indefinitely without cultivation. It is true, as already mentioned, that at regular intervals the marsh is generally plowed, but this is by no means to aid these grasses in their competition with other plants, but is mainly to renew the stock on special places to keep it up to the very highest condition of productive vigor. The case of marsh not plowed for over forty years, and still bearing the English grasses with apparently undiminished vigor, shows that the plowing is not essential. Man, therefore, has both created a new field by diking the marshes, and has also brought in a vegetation better fitted than any native vegetation for that field. Later the question of why this introduced vegetation is better than any native kind for this situation will be discussed.

It is an interesting question as to what appearance these great expanses of marsh would present today had man never reclaimed them. We cannot doubt that they would be salt marsh like the still unreclaimed pieces. The fact that the marshes are still sinking, or at least are not rising, would prevent any natural recovery and building up by the action of large vegetation, such as is occurring at the mouth of the Rhone, as described by Flahault and Combres, though were the region rising such a result would probably occur.

As to other animals on the marshes, insects seem fairly abundant, and of course play their part in the pollination of the plants which have showy flowers, but as the greater part of the vegetation is anemophilous, or wind-pollinated, their influence is not ecologically important. Birds occur as in upland meadows. Mosquitoes are abundant and voracious. Various fishes occur in the ditches and canals, and frogs and muskrats are abundant in the fresh-water streams. None of these appears to have any

determinable influence upon the vegetation. An animal important in the economy of soils, namely the common earthworm, is said by the residents not to occur upon the marshes. I have seen what appeared to be their castings, but have been told by an intelligent observing farmer that these are in reality made by some burrowing insect.

Geography of the basin.—To the ecological factors already considered there must be added another of a different sort, namely, the geography of the basin itself. We have already considered one phase of this subject, for upon the latitude, elevation, proximity to the sea, to cold or warm ocean or air currents, depend some of the ecological factors previously discussed. But in addition there are two other important phases of the subject. First, there is the geographical position of the region relative to the great floristic divisions of the earth's surface, upon which depends its flora (as distinct from its vegetation, which is determined by the preceding), and the flora determines the materials upon which the particular ecological factors of the region are to work. In this case we are dealing with a portion of the region covered by the temperate North American flora, with all the peculiarities of species, genera, and families thereto belonging. Second, there is the degree of isolation of the basin from the neighboring regions. Isolation may be brought about principally by the presence of natural barriers, mountain ranges, wide arms of the sea or desert, or even to some extent by great size. Isolation is ecologically important, for upon it depends the possibility of the rapid development of indigenous and exceptionally adapted forms. It produces this result both by preventing the dilution of new adaptive characters through crossing with immigrants from without, and also by preserving undiluted those characters which may be developed independently of adaptation. Regarding now the marsh country from this point of view, we see at once that it is entirely without natural barriers of any kind, and lies open in every direction to immigration from sea-shore, field, and forest; while it is so small in extent (nowhere exceeding four or five miles in diameter), that the natural modes of locomotion of most of the plants

round about can carry them readily to every part of it. Under these circumstances there is not, nor can there be in the marshland, any development of extreme adaptations, much less of new types. What happens is this—the ecological conditions here prevailing select from the great mass of forms which are constantly brought to them by natural modes of dissemination, the particular forms that happen to be best adapted to those conditions, rejecting, by suppression, all others. Further, as I believe, having selected the best adapted, their adaptations are in such a basin improved and intensified, so that these forms are being distributed from the basin in a better adapted condition than they enter it. Probably it is a general rule that the larger and more isolated the basin the more the tendency to develop peculiar types; the smaller and less isolated the basin, the more is it a case of selection of forms brought constantly into it and their improvement, such small basins serving as centers of distribution of better adapted forms. The ecological interest of these marshes lies, not in any peculiar adaptations they show, but in the perfection with which they exhibit many phenomena of adaptation.

Summary of the ecological factors: the responsive type of vegetation.

The various physical features we have just considered constitute a set of conditions to which the vegetation must conform. Since no development of a special vegetation to fit them is possible, we ask what forms of the plants of this region do come nearest to fitting those conditions and hence actually occur there. So far as the general climatic conditions are concerned, the responsive type for this region, as I have elsewhere shown,[32] is a mixed mesophytic forest, such as actually occurs on the neighboring uplands. But on the marshes there comes in another factor which is of the first importance and is prepotent or determinative, namely, the peculiar soil. This requires that the marsh vegetation shall be such as has a superficial or very slender root

[32] The vegetation of New Brunswick as a whole I have considered in Bull. Nat. Hist. Soc. New Bruns. 5:52. 1903.

system, thrives in a siliceous and somewhat salt soil, needs a constant rather than a great water supply, can spread a mesophytic foliage to the summer sun and retreat to a winter xerophytic condition, can endure exposure to unshaded sun and strong winds and not spread too great a surface to their transpiring influence, and can use the wind in dissemination and cross-pollination. No one form of vegetation can be found to fit best all these conditions, but any ecologist can tell at once what type comes the nearest to fitting them in the aggregate; it is the grasses and grass-like plants. This is why the vegetation of the marshes is so overwhelmingly of that kind.

The plants of the marshes.

We turn now to consider in some detail the vegetation of the marshland, and naturally ask first what kinds of plants live there. No attempt has yet been made to prepare a flora of the marshes, and such scanty lists of species as exist have already been mentioned (page 162). From the point of view of ecological plant geography, however, their floristic completeness is of slight importance, since the character of the vegetation is determined by only a few prominent forms, and all of those rarer and less conspicuous species, naturally of such interest and importance to the floristic student, might be wanting without affecting the characteristics of the vegetation as a whole. Further, the species, as such, are not of special concern ecologically. What is here important is this, the species as an aggregation of adaptations, that is, as a vegetation- (or life-, or biologic) form, for these vegetation-forms are the unit of the ecologist as the species are of the systematist. In a general way species and vegetation-forms may not be coincident. Thus the same vegetation-form may be developed under similar ecological conditions from very different and widely separate species, as witness Agave-Aloe, Calluna-Erica, and Cereus-Euphorbia (some), but this does not hold true in minutiae, and such forms as those above mentioned, while alike in most characters, differ in many particulars. This is of course because plants are not indefinitely plastic to environmental influences, but are limited much

in adaptation by their heredity, and a different heredity does not permit two distantly related plants to be brought into ecological identity at all points. Hence for purposes of detailed ecological study, and as well because of practical convenience, species and vegetation-forms are coincident, though the point of view from which they are regarded by systematist and ecologist is different. This treatment of the two as coincident is the more necessary at present because of the undifferentiated state of knowledge and terminology of the vegetation-forms,[33] a subject greatly in need of systematic study and formulation. In the following pages I have attempted to indicate a few of the characteristics of the principal species[34] treated as vegetation-forms, especially in the case of *Spartina stricta*, and the ill-success of the attempt is at least in part due to the imperfections in our knowledge of this subject, a matter on which further comment will be found later in this paper. Much work has of course been done upon the anatomy of all of these plants, and Kearney has summarized it in some of the forms, but I have not attempted to treat this phase of the subject.

The vegetation of the marshland.

The vegetation-forms of any region taken together constitute its vegetation. The units, however, are by no means mixed at random to form the mass, but are grouped differentially in

[33] This term, used by Pound and Clements, while better than the "life-forms" of Smith and the "biologic forms" of the translation of Flahault, is far from satisfactory, since the word *form* is somewhat ambiguous and the phrase does not convey an idea of the real significance of the vegetation-form either as a unit of the vegetation, or as a resultant of adaptations. A proper terminology of vegetation-forms (a beginning in which has been made by Pound and Clements) is especially needed in order to allow the forms of different countries to be compared, which they cannot be if simply named for their species.

[34] All of the species listed in the following pages, unless otherwise mentioned, have been confirmed or determined by Mr. Walter Deane, of Cambridge, Mass., with the exception of a few of the grasses which have been named by Mr. F. Lamson Scribner, of Washington, and to both of these botanists I must express my sincere thanks for their kind aid. The English names given are in all cases those by which the plants are locally known in the marsh country. The nomenclature is that of the sixth edition of Gray's Manual, to which in brackets are added the synonyms made use of in Britton's Manual.

accordance with definite factors. This grouping, and its causes, so far as known, we have now to consider for the marshland.

The vegetation of any region develops, in response to the great primary ecological factors of temperature and precipitation, a characteristic climatic type, which prevails wherever no limiting factor becomes prepotent. For the region in which the marshland lies, this type is a mixed mesophytic forest, as shown upon the neighboring uplands. Further, according to Cowles' theory, which seems to me in general well-grounded, all the vegetation of a region is tending to approach this type, because the vegetation is very closely correlated with physiographic factors, and physiographically any region is in general tending to approach a base-level uniformity. This tendency involves the elimination of prepotent secondary factors, and hence the approach of the vegetation to the climatic type. The marshes appear to offer an exception to this rule, an exception more seeming than real, as will later be noticed.

On the marshland, however, certain limiting factors do become prepotent, determining marked deviations from the climatic type and hence divisions of the vegetation as a whole, namely, *the presence of abundant salt in the soil*, determining a HALOPHYTIC DIVISION, *an accumulation of fresh water* determining a HYDROPHYTIC DIVISION, and *the influence of man*, which removes large sections from the halophytic to the MESOPHYTIC DIVISION, or rather to a special section of it which may be called the *culture section*. The fourth of the principal vegetation divisions, the xerophytic, is not represented in the marshland. These divisions, however, are by no means of homogeneous appearance, but their vegetation falls into distinct groups of plants, the prominent forms of which have the same general aspect and adaptations, and occupy and are correlated with distinct physiographic positions. Such groups are called *formations*. They usually form distinct features of the landscape, and are known by distinctive local names expressing the physical habitat, such as bog, marsh, etc. But the formations, more closely observed, do not show an even mixture of plants, for these are grouped or segregated into definite assemblages, dependent in some part

upon degrees of the physical factors determining the formations, though in larger part upon a quite different principle, namely, the ecological interrelationships of the plants to one another, particularly with reference to the ability of different forms to occupy the same ground at the same time without serious interference and perhaps with positive benefit to one another. Such groups are called appropriately *associations*, and they often are recognized and named locally by the prominent forms, such as oak-forest, broadleaf marsh, etc. Formations and associations are thus both distinct ideas and distinct groups, the former having the physical or physiographic idea prominent, and the latter the idea of ecological interrelationships of the plants, involving their competition and cooperation. Of course the two merge into each other, and often coincide, and by many students they are treated as one. Their delimitation, while often easy, is sometimes very difficult. As in all such cases they can be studied and described only by the selection of typical examples, all intermediate forms being described in terms of the typical. The associations are made up of the *vegetation-forms*, the ecological units, best treated for the present, as above explained, as coincident with species. These vegetation-forms constitute the *members* of the association, but of varying degrees of importance. Some are evidently far in the lead in size, numbers and importance — they are dominant; others are close to these and struggling for the leadership — they are secondary; others are much less conspicuous, but manage to maintain a position among the preceding in spots not occupied by them — they are subordinate. Then in addition to the members may be recognized the frequent visitors from neighboring associations, and various strangers or stragglers from more distant positions. But a satisfactory terminology of the degrees of membership must await an understanding of the real nature of their interrelationship, a knowledge which we do not yet possess.[35]

[35] The distinction here drawn between formations and associations will not be admitted as valid by all, at least to the degree here held, but I believe it represents a real fact in nature and will stand. There is moreover an increasing tendency to recognize the distinction as well as to use this terminology. It is used by Kearney, by Lloyd and Tracy, and by Harshberger (though he calls the association a society).

The various associations of the marshland, named according to their dominant forms, together with their formations to which they belong, are shown by the following synopsis.

Clements lays much stress upon the formation, but gives the association a subordinate place, designating it as "patch." Cowles recognizes formations (under the name of society) but gives no separate importance to the association. Smith recognizes the formation under the name of association, but combines features of both. Warming recognizes the formation (calling it *Verein*), but hardly the association as a distinct group; and the usage is similar in Schimper and Drude. In all these cases, where the one is distinguished and not the other, the facts are of course recognized, though the two groups of ideas are consolidated as it were into one. In such cases the idea of the association is often brought out as a "facies," etc. The complicated history of the use of these terms may be traced in the works of Smith and Flahault cited in the bibliography. The words formation and association as here used seem to me good terms, and should be adopted. The word society could better be restricted to those ecological groups of another kind, such as epiphytes, parasites, etc. Clements has recently made a carefully considered proposal for nomenclature of formations, and I have given some of his names later in this paper. The associations are best distinguished by their dominant forms with the termination *etum*.

[*To be continued.*]